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Anniversary Essay

# Winning, losing, and reaching out

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Here, we argue that behavioral ecologists can do even more than we have done to facilitate new, interdisciplinary collaborations. Our argument is a general one, but we focus on how to do this with winner and loser effects. We develop a new, general model of winner and loser effects as the outcome of flexible decisions about how much to invest in competition and discuss the model's implications for overall levels of conflict within a species. Finally, we argue that winner and loser effects is a topic ripe for fostering collaborations with researchers in cultural anthropology and sports psychology.

*Key words*: **game theory, loser effect, tug-of-war model, winner effect.**

We would be rude and remiss if we did not start off with the appropriate salutation on an occasion such as this: Happy 25th anniversary, dear *Behavioral Ecology*! Perhaps it sounds overly emotional, but both of us *love* being behavioral ecologists, and we think *Behavioral Ecology* is a wonderful representative of our cherished discipline.

The field of behavioral ecology, which seeks no less than to understand how ecology sets the stage on which natural selection acts on behavior, has grown by leaps and bounds since this journal was initiated. One of the many ways this has happened is by behavioral ecologists reaching out to those in related, and sometimes seemingly unrelated, disciplines—cognitive psychology, biological anthropology, mathematics, economics, and political science, to name just a few—and fostering collaborations, with the long-term goal of a deeper understanding of the roots of behavior. Not surprisingly, when such links are first established, each side can be reluctant to take the perspective of the other; but in time, open-minded scientists, after heated discussions, sort through all that. We applaud this aggressive, interdisciplinary, collaborative approach and we try to take it ourselves—indeed, it is one of the many reasons we are behavioral ecologists.

In this article, we simply want to make the case that behavioral ecologists can, and should, do even more to facilitate new, interdisciplinary collaborations. Our argument is a general one, but as a case in point, we focus on the winner and loser effects that behavioral ecologists have been studying from both proximate and ultimate perspectives, expand this work by developing a new, general model of winner and loser effects and their implications and argue that this topic is ripe for fostering collaborations with researchers in cultural anthropology and sports psychology.

## WINNER AND LOSER EFFECTS AND DOMINANCE HIERARCHIES

In many species, individuals spend a portion of their lives living in groups of one sort or another. Though "group" can be a tricky term to operationally define, here we mean a set of individuals whose behavior affects each other's fitness (Wilson 1980). One striking aspect of group life is the presence of aggressive interactions among its members. If groups are stable and relatively long lived, aggression often manifests itself in the form of a dominance hierarchy.

Biologists' interest in the nature of dominance hierarchies can be traced back at least as far as Schjelderup-Ebbe's seminal work on this subject in chickens (Schjelderup-Ebbe 1922). Behavioral ecologists' interest in hierarchy formation and hierarchy stability is in part due to one counterintuitive, or at least perplexing, aspect of such hierarchies: if hierarchies are stable, why would an individual in a group ever "accept" a role other than that of alpha (highest ranking) individual in its group?

The answer must revolve around the specific costs and benefits associated with positions in a hierarchy, and so hierarchy formation and stability have been studied across many taxa, both in terms of gauging these costs and benefits and by examining the hormonal underpinnings of the aggression associated with dominance hierarchies. Dominance hierarchy formation has also been tackled from a theoretical perspective, with many different mathematical models developed to help understand this salient component of group living.

Both intrinsic and extrinsic factors impact fighting behavior and dominance hierarchy formation (Landau 1951a, 1951b). Intrinsic factors correlate with an animal's resource holding potential or RHP (Parker 1974). The predominant way that behavioral ecologists examine intrinsic factors is by testing the effect of an animal's size on its probability of winning fights and maintaining a high position in a hierarchy.

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Work on how extrinsic factors affect aggression and dominance hierarchies has generally focused on what are known as winner and loser effects (Landau 1951a, 1951b; McGregor et al. 1999; McGregor and Peake 2000; McGregor 2005; Hsu et al. 2006, 2009; Hock and Huber 2009; Fawcett and Johnstone 2010; Fuxjager and Marler 2010), though a more general social network approach to extrinsic factors has been emerging recently (Croft et al. 2008, 2011; Krause et al. 2011; Bode et al. 2012; Jacoby et al. 2012; Wilson et al. 2013). Winner and loser effects are defined as an increased probability of winning at time T, based on victories at time T-1, T-2, and so on, and an increased probability of losing at time *T*, based on losing at time T-1, T-2, etc., respectively.

Winner and/or loser effects have been found in many species—from insects and crabs to birds, snakes, lizards, and mammals (Dugatkin 2013)—and behavioral ecologists are beginning to understand both the costs and benefits associated with these effects, and the proximate underpinnings of winner and loser effects, by studying both baseline levels and changes to such hormones as cortisol and testosterone (Oliveira et al. 2009; Chang et al. 2012; Earley et al. 2013).

Though much of the work on winner and loser effects is done under controlled settings in the laboratory, there are some studies in the field. On Isla Isabel, Mexico, Drummond and his colleagues investigated the role of winner and loser effects during nest mate hierarchy formation in blue-footed boobies (*Sula nebouxii*) (Drummond and Osorno 1992; Drummond and Canales 1998; Drummond 2006; Benavides and Drummond 2007; Gonzalez-Voyer et al. 2007). Drummond's early studies in this system *hinted* at winner and loser effects: if older chicks were aggressive early on in development, and younger chicks were submissive during this stage, older chicks would subsequently defeat younger chicks (Drummond and Osorno 1992). Of course, it is possible that no winner or loser effects were in play and that this can all be explained by initial differences in the RHP of older and younger chicks. What's more, even if extrinsic factors were important, because older and younger chicks were pitted against one another, it was not possible to determine if loser effects (in younger chicks), winner effects (in older chicks), or both played a role in establishing hierarchies in this species.

Drummond and Canales (1998) ran a follow-up experiment to untangle all of this. They paired older, aggressive, dominant birds and younger, subordinate birds against *inexperienced* partners. They predicted that subordinate animals that were paired with inexperienced partners (who came from single egg clutches) would have a low probability of winning aggressive bouts, and to be conservative, the inexperienced individuals used were smaller than the subordinate individuals (presumably *increasing* the subordinate's chance of victory). They also pitted older, aggressive birds with inexperienced partners and predicted that the older aggressive individuals would have a high probability of winning future aggressive interactions (dominant individuals were paired with slightly larger inexperienced individuals).

What Drummond and Canales found was that subordinates were 7 times *less* aggressive than were their inexperienced pairmates, providing strong evidence of winner effects, and dominant birds were 6 times *more* aggressive than their pairmates, indicating a true loser effect: over time, the winner effect dissipated, but the loser effect did not.

In addition to many empirical studies, there is a growing theoretical literature on winner and loser effects. In the earliest modeling work on extrinsic effects, Landau examined how these effects, in conjunction with intrinsic factors, explain why many dominance hierarchies are linear and transitive: individual A typically defeats individual B, B typically defeats C, and A defeats C (Landau 1951a, 1951b). Landau found that intrinsic factors alone usually did not produce linear hierarchies, but if he added in winner and loser effects to his model, linear hierarchies often emerged.

Subsequent models have been built on the framework first constructed by Landau. For example, Landau's models did not allow winner and loser effects to act independently of each other (either a winner and loser was in place or neither was), and individuals were not capable of gauging each other's RHP. In addition, Landau's models only considered one type of aggressive interaction: an actual fight between contestants. But aggressive interactions can also take more subtle, potentially less costly forms, such as "one individual attacks, and its opponent retreats." Second-generation models have allowed for such complexities and have shed new light on winner and loser effects and how they affect dominance hierarchies (Chase 1974, 1982; Bonabeau et al. 1996, 1999; Skvoretz et al. 1996; Hemelrijk 1999; Beacham 2003; Lindquist and Chase 2009; Chase and Seitz 2011). For example, when winner and loser effects operate independently, these effects predict different types of hierarchies. Winner effects alone lead to hierarchies in which all individuals hold unambiguous ranks and most aggressive interactions are fights (rather than attack–retreat sequences). Loser effects, in the absence of winner effects, produce a clear top-ranked (alpha) individual, but a hierarchy in which the rank of others is unclear. In such hierarchies, the vast majority of the interactions are predicted to be attack–retreat sequences (as opposed to fights) (Dugatkin 1997).

A different family of models has tackled winner and loser effects from a game theoretical perspective. Rather than assume the existence of winner and loser effects and then examine the type of hierarchy that emerges, these models ask whether winner and loser effects are evolutionarily stable strategies. In general, these models predict that loser effects are an evolutionarily stable strategy (ESS), but winner effects are only evolutionarily stable if loser effects are also in place. That is, we expect systems in which loser effects or winner and loser effects are present, but not systems with only winner effects (Mesterton-Gibbons 1999; Hock and Huber 2009; Mesterton-Gibbons and Sherratt 2009). The empirical literature suggests that this is what we find in nature although there are exceptions (Goubault and Decuigniere 2012).

## BROAD IMPLICATIONS OF WINNER–LOSER EFFECTS FOR WITHIN-GROUP CONFLICT

Winner and loser effects are not really strategies but rather outcomes of the joint investments of the competing parties in competition; that is, the probability that I win a fight with an opponent depends not only on my fighting ability but also on how much effort I invest in the fight *relative to* the investment of my opponent. The evolutionarily stable efforts in such scenarios are best modeled separately from each other and then combined to see what the outcome will be. Tug-of-war theory and earlier theories such as the asymmetric war of attrition (Hammerstein and Parker 1982) are ideally suited to modeling these mutual, optimal, competitive investments (Reeve et al. 1998). Here, we will show that tug-of-war models of winner–loser effects unveil a particularly important society-wide implication of winner–loser effects: in social groups where such effects are present, the mean fitness of individuals will always be higher than in social groups where they are absent. In short, these effects ameliorate the "tragedy of the commons" that usually results from social competition (Hardin 1968).

Consider a competitive interaction between 2 parties competing over a resource such as food or mates. Each party must decide how much effort to invest in competition, with the fraction of the disputed resource accruing to each party dependent on their relative investments in competition. The invested efforts come at the expense of some other fitness component, and the rate at which competitive effort reduces this component—the cost rate—differs between the 2 individuals. The cost rate for the weaker individual is higher than the cost rate for the stronger individual, reflecting that weaker individuals must pay more in energy, risk, and so on to achieve a competitive effort that matches the effort of its partner. The cost rate can be thought of as being inversely related to the individual's competitive ability. Thus, an individual that signals a lower cost rate for itself is in effect signaling a higher competitive ability.

Let the competitive effort of a competitively superior individual (dominant) be $x$ and that of the competitively inferior (subordinate) individual be $y$. The resource is of value $V$, and the fraction won by the dominant is $x/(x + y)$. This is a tug-of-war model because the outcome of competition depends on the *relative* competitive investments instead of the absolute competitive investments. The cost rate for the dominant is $a$ and that of the subordinate is $b$, with $b > a$. Thus, the fitness $w_d$ of the dominant and $w_s$ of the subordinate are given by:

$$w_d = \left(\frac{x}{x+y}\right)V - ax, \quad w_s = \left(\frac{y}{x+y}\right)V - by \tag{1}$$

## Winner–loser effects absent

Let us first assume that in a hypothetical world without winner and loser effects, each player has no precise knowledge of either its own or its opponent's cost rates (i.e., relative competitive ability). As far as either the dominant or subordinate knows, its expected fitness $w$ is just:

$$w = \left(\frac{x}{x+y}\right)V - ux \tag{2}$$

where $u$ is the mean cost rate for all individuals in the pool of competitors. This fitness equation holds for both the dominant and the subordinate, and the evolutionarily stable (mutually optimal) efforts are:

$$x^* = \frac{uV}{(u+u)^2} = \frac{V}{4u}, \quad y^* = \frac{uV}{(u+u)^2} = \frac{V}{4u} \tag{3}$$

Thus, the ESS efforts are the same for all competing individuals, whether dominant or subordinate in a given interaction. Plugging these ESS efforts into Equation 1 yields a fitness of $(2u - a)V/4u$ for the dominant and $(2u - b)V/4u$ for the subordinate. The expected value for the fitness across all competing individuals is then $(2u - u)V/4u = V/4$.

## Winner and loser effects present

Now, we imagine a population in which individuals engage in multiple pairwise contests and, as envisioned in winner–loser effects, are increasingly able to assess their cost rates (competitive abilities) relative to each other, which are then used to set the competitive efforts that will determine the outcome of the competition. These assessments converge to the true cost rates and allow the contestants to fine-tune their competitive investments to their relative competitive ability.

Here, we solve for the optimal competitive investment of each as a function of its own competitive ability, its opponent's competitive ability, and the competitive effort of the opponent. In effect, each player is gradually able, through repeated interactions, to deduce or observe $a$, $b$, and $x$ (or $y$). The evolutionarily stable efforts are obtained by jointly solving $\mathrm{d}w_d/\mathrm{d}x = 0$ and $\mathrm{d}w_s/\mathrm{d}x = 0$. This yields the evolutionarily stable efforts:

$$x^* = \frac{bV}{(a+b)^2}, \quad y^* = \frac{aV}{(a+b)^2} \tag{4}$$

Substituting Equation 4 into Equation 1 yields the fitnesses for the dominant and subordinate at equilibrium, that is, $w_d^*$ and $w_s^*$, respectively. These are:

$$w_d^* = \frac{b^2V}{(a+b)^2}, \quad w_s^* = \frac{a^2V}{(a+b)^2} \tag{5}$$

The ESS competitive efforts in Equation 4 entail winner and loser effects. When 2 contestants with no information about their competitive abilities (inversely measured by their cost rates) first interact, their competitive efforts are $V/4u$ (see Equation 3), where $u$ is the mean cost rate for the population. However, after multiple interactions in which they can assess their relative abilities, the competitive efforts are the solutions given in Equation 4. Because the dominant's cost rate $a$ is less than the subordinate's cost rate $b$, it is easily shown that the dominant's new effort in a later interaction must be greater than the subordinate's effort. This divergence in efforts automatically leads to a type of winner and loser effects, that is, to an increased probability of the dominant winning the competition with time (and, of course, a decreased probability for the subordinate winning it).

Importantly, on average, in our model, individuals do better in a world with winner–loser effects than in one without them. The mean fitness in a population without winner–loser effects is $V/4$ (see above). In a world with winner–loser effects, the joint fitness of a pair of competitors is always $V(a^2 + b^2)/(a + b)^2$, which is the sum of the 2 fitnesses in Equation 5. It is easy to show that this sum is always greater than or equal to $V/2$, for every interaction, meaning that the average fitness of individuals must be greater than $V/4$ if there is any variation in competitive abilities in the population (if the 2 individuals have exactly equal competitive abilities, i.e., $a = b$, they each have a fitness exactly equal to $V/4$). Thus, individuals always do better on average in populations with winner–loser effects. Moreover, the greater the variation in competitive abilities in the presence of winner–loser effects, the greater the increase in individual fitness and thus total group reproductive output. There is evidence for the latter prediction from social insects: paper wasp (*Polistes dominulus*) groups of cooperating foundress females contribute more per capita to colony growth the greater the variation in body size (a predictor of fighting ability) within the group (Nonacs and Reeve 1995).

In sum, winner–loser effects lessen the destructiveness of the tragedy of the commons that often results from competition. This may have implications for how group composition will be manipulated by group members who benefit when there is greater or lesser competition in the group. For example, a dominant member of a society might benefit from promoting variation in competitive ability in group members if the dominant reaps more benefits from a peaceful group.

# USING WINNER AND LOSER EFFECTS TO REACH OUT

We are of the notion that everything that behavioral ecologists study in nonhumans is likely relevant to understanding the evolution of human behavior, even if, in some instances, only indirectly. That said, there may be certain areas of behavioral ecology that allow more natural bridges to form with those who study human behavior in other fields. That was certainly the case in the early days of behavioral ecology when those working on the evolution of foraging behavior had some common ground with psychologists using operant conditioning protocols that often revolved around animal foraging behavior.

Work on the behavioral ecology of winner and loser effects may also help us form new collaborations with those who seek to understand human behavior in other disciplines. Two such disciplines are cultural anthropology and sports psychology.

## Cultural anthropology

Through well-placed review articles, and perhaps targeted, small interdisciplinary workshops, behavioral ecologists could introduce cultural anthropologists to the nonhuman literature on winner and loser effects and their implications for hierarchy formation. We could then open a dialogue on the ways that our models of winner and loser effects could be modified by layering on the subtle complexities and intercultural differences in which cultural anthropologists specialize. As one possible example, when winner effects alone are at play, models suggest that fights are predicted. When only loser effects are in play, these models predict much less intense aggression because of an increase in "attack–retreat" sequences. The degree of aggression in human populations is a major area of interest in cultural anthropology, but the relationship between aggression and winner effects and loser effects has not been examined in the cultural anthropological literature. One way for behavioral ecologists and cultural anthropologists to begin to work together on the impact of winner and loser effects in humans would be through the use of the Human Relations Area Files (HRAF) (http://www.yale.edu/hraf/).

The HRAF is a huge, searchable, multicultural database—the most comprehensive of its kind in the world—that has information on aggression in human societies from across the planet (e.g., Daly and Wilson 1988 used this database for their work on homicide). Although the HRAF does not have entries on winner and loser effects, the data that it contains could be used to make some inferences about such effects in human populations. When behavioral ecologists and cultural anthropologists work together through the HRAF, new questions about winner and loser effects will hopefully arise. What those questions will be a priori is hard to say, but whatever they are, our hope is that they will generate new models and new tests of winner and loser effects and open the door for further collaborations between cultural anthropologists and behavioral ecologists, including generating new ideas for researchers in both disciplines to test in humans and nonhumans.

## Sports psychology

The field of sports psychology boasts numerous journals, including the *Journal of Sport Psychology in Action*, which lists its mission as "to promote the application of scientific knowledge to the practice of sport, exercise, and health psychology." Behavioral ecologists could introduce the animal literature on winner and loser effects and their implications for hierarchy formation to sports psychologists and suggest ways models could be tested in human sporting events where teams are structured into leagues (potential hierarchies), but play one-on-one matches or games to determine position in a league (allowing for winner and loser effects).

The sports psychology community seems ripe for a collaboration with behavioral ecologists because:

1. Sports psychologists have a long-standing interest in wining and losing "streaks" that are at the heart of winner and loser effects (Albright 1993).
2. Recent publications in sports psychology suggest a genuine curiosity about the implications of winner and loser effects and hierarchy formation in sports from hockey and rugby to badminton, but no theoretical framework for understanding how these phenomena affect human behavior (Carre and Putnam 2010; Widermann et al. 2011; Allen et al. 2012; Cook and Crewther 2012; Crewther and Cook 2012; Jimenez et al. 2012).
3. The evolutionary principles described above might also help sports psychologists to understand not only the results of game competition but also the structure of competitive leagues. For example, league owners might benefit from rules ensuring league parity (evenness of competitive ability among teams) when their profits are directly linked to increased competitive efforts (e.g., acrobatic catches and crunching tackles) of individual team members (see above).
4. Sports psychologists have access to, and a deep understanding of, the many detailed statistical databases on athletic performance (such as wins and losses). One example of this sort of readily accessible database is the Sabermetrics baseball database (http://sabr.org/) that became famous with success of the movie *Moneyball*.

A collaborative analysis between behavioral ecologists and sports psychologists on winner/loser effects and dominance hierarchy formation using databases like Sabermetrics could lead to new models and experiments in humans and nonhumans alike.

Let's make these sorts of collaborations, and many others, happen.

**Editor-in-Chief:** Leigh Simmons

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